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Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services

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SUMMARY

Despite the fact that migratory insects dominate aerial bioflows in terms of diversity, abundance and biomass [1–6], the migration patterns of most species, and the effects of their annual fluxes between high and low latitude regions, are poorly known. One important group of long-range migrants which remain understudied are a suite of highly beneficial species of hoverfly in the tribe Syrphini, which we collectively term '*migrant hoverflies*'. Adults are key pollinators [7–10] while larvae are significant biocontrol agents of aphid crop pests [11], and thus it is important to quantify the scale of their migrations, and the crucial ecosystem services they provide with respect to energy, nutrient and biomass transport, regulation of crop pests, and pollen transfer. Such assessments cannot be made by sporadic observations of mass arrivals at ground level, because hoverflies largely migrate unnoticed high above ground. We used insect-monitoring radars [12] to show that up to 4 billion hoverflies (80 tons of biomass) travel high above southern Britain each year in seasonally-adaptive directions. The long-range migrations redistribute tons of essential nutrients (N and P) and transport billions of pollen grains between Britain and Europe, while locally-produced populations consume 6 trillion aphids and make billions of flower visits. Migrant hoverfly abundance fluctuated greatly between years, but there was no evidence of a population trend during the 10-year study period. Considering that many beneficial insects are seriously declining [7, 10, 13–19], our results demonstrate that *migrant hoverflies* are key to maintaining essential ecosystem services.

RESULTS AND DISCUSSION

Trillions of high-flying migrants make long-range movements into high-latitude temperate regions each spring, before they and/or their progeny return to lower latitudes the following autumn. These mass aerial 'bioflows' result in the aerial transport of massive amounts of energy and nutrients between distant regions, whilst the huge seasonal influxes of potential prey, herbivores, pollinators, predators and parasites have profound impacts on local food-webs, community dynamics and provision of ecosystem services [1–6]. The migration routes, total abundance and seasonal patterns of migration intensity are comparatively well understood for birds [20–23], but we know much less

about insect migrations. A recent radar study of insect migration high above southern Britain [3] revealed that between 10–25 billion medium (body mass 10–70 mg) and large (70–500 mg) insects, comprising ~300–1000 tonnes of biomass, undertake bidirectional movements into and out of this region each spring and autumn. The British study demonstrated that ~70% of directed migrations of high-flying larger insects occurs during the daytime, and involves mostly beneficial or non-pest species [3], but until now radar studies of windborne migration of specific taxa have almost exclusively focused on night-flying migrants and pest species [2, 12, 24–26]. Given the widespread evidence that non-migratory beneficial/non-pest insect populations, particularly pollinators, are undergoing serious declines around the globe [7, 10, 13–19], annual arrivals and departures of migratory insects may play increasingly important roles in maintaining ecological networks and the provision of beneficial services such as pollination and pest control.

One group of insects which are potentially key in this respect are hoverflies (Diptera; Syrphidae). Some common European species in the subfamily Syrphinae and tribe Syrphini, particularly *Episyrphus balteatus* and *Eupeodes corollae*, are highly migratory (see Tables S1 and S2), with prodigious numbers migrating into and out of Northern Europe on an annual basis [27–33]. This suite of species, hereafter collectively referred to as '*migrant hoverflies*', are extremely abundant components of insect communities in temperate latitudes [34–36], and they play two vitally important roles in these environments: adults are important pollinators [7–10, 36], while their larvae are voracious predators of pest aphids [11, 37]. Hoverflies have long been recognised as long-range, diurnal migrants [27–33], but all published descriptions are of mass flights at ground level, with no quantification of the situation aloft. The inability to monitor high altitude hoverfly migration means there have been no systematic studies of windborne migration directions and intensities, or estimates of the effects of mass influxes and subsequent departures on ecosystem processes and services, in this important group of migrants. We address this knowledge gap by determining seasonal patterns of high-altitude migration of the most common species of *migrant hoverflies* (Tables S1 and S2) into and back out of southern Britain, and by estimating the impacts of their mass arrival on pollination and pest control services.

Vertical-looking entomological radar (VLR) data [10, 25] were used to quantify annual abundance and biomass flux of *migrant hoverflies* high above a 300-km wide (70,000 km²) region of southern

Britain (Figure 1A) over a 10-year period. The VLR data was filtered to match the body mass (Table S1), body shape based on radar reflectivity values (Table S2) [38], and diurnal flight timing of the most abundant European migratory hoverfly (*E. balteatus*, see Tables S1 and S2), but the dataset likely includes a small proportion of other relatively abundant migratory species in the tribe Syrphini with overlapping physical characteristics (e.g. *E. corollae*; see STAR Methods, Tables S1 and S2). This data selection resulted in >365,000 individual VLR-detected *migrant hoverflies* (Table S3) taken forward for further analysis. Confirmation of the reliability of our measure of hoverfly migration is provided by the close relationship of half-monthly VLR data with combined counts of *E. balteatus* and *E. corollae* in the same periods from the Hoverfly Recording Scheme (HRS) in each of the 10 study years (Figures 1B and S1), and the correlation between these datasets was highly significant when aggregated across all 10 years ($p < 0.0001$, Figure 1C). Within our radar sampling range, between 150–1200 m above ground level (agl), hoverfly density was greatest at the lowest altitudes (<300 m agl) but with considerable numbers migrating up to 750 m agl (Figures 1D and S2).

Seasonal patterns of migration direction were quantified by analysing migratory tracks (the windborne displacement directions) during 615 'mass migration events' (see STAR Methods). The mass migrations included 75% of the total radar counts (273,000 individuals) in just 23.4% of the total migration occasions (Table S3). *Migrant hoverflies* first appeared in early-May and numbers gradually built up over the next 2 months (Figures 1B and S1). During this time, track directions of the mass migrations were consistently towards north in each of the 4 half-monthly periods of May and June (tracks between 300° and 350°, Table S3), with an overall mean spring track direction towards NNW (Rayleigh test, mean track = 342°, n = 186 mass migration events, $r = 0.53$, $p < 0.001$, Figure 2), consistent with immigration into southern Britain from the near continent. We therefore categorised May and June as the 'spring immigration' phase, and the flies detected in this period represent the first generation reaching Britain. Hoverfly abundance continued to increase during July as the second generation appeared (the progeny of the original immigrants), but during this period there was no clear seasonal pattern of migration direction. The distribution of tracks was random in early-July, and with a slight tendency towards the SE in late-July (Table S3); this SE bias was also present in the combined data for the whole of July (mean track = 151°, n = 181, $r = 0.24$, $p < 0.001$, Figure 2), albeit with a wide spread of directions (signified by the low r-value). Due to the lack of

consistent migration directions during this season, we categorised July the 'mid-summer dispersal' phase, a phenomenon seen in other diurnal and nocturnal migrants [3, 39]. During August and September, records of our focal species started to decline (Figures 1B and S1) as the 1–2 locally produced generations [40] departed southern Britain. Mass migration events were consistently directed towards the south in each of the 3 half-monthly periods with enough data (Table S3), with an overall mean autumn direction of precisely due south (mean track = 180°, n = 248, r = 0.43, $p < 0.001$, Figure 2). The predominance of southward tracks in the autumn does not match the pattern of prevailing winds, which consistently blow towards the NE throughout the year [3]. The autumn migration tracks are thus indicative of active selection of favourable high-altitude tailwinds by the hoverflies to facilitate mass return movements to lower latitudes, and we therefore categorised August and September as the 'autumn emigration' phase. *Migrant hoverflies* thus clearly demonstrate active selection of seasonally-beneficial winds for their mass spring and autumn migrations, and achieve seasonal reversal of their migration directions in much the same way as larger migrant insects (e.g. noctuid and sphingid moths, nymphalid butterflies) [3, 24–26, 41, 42].

The high-altitude, seasonally-directed hoverfly migrations occur on an enormous scale. Our data demonstrate that over the 10-year study period, the mean total travelling high above our 300 km wide study region was 2.66 billion hoverflies per year (range: 1.36 to 3.99 billion, Figure 3 and Table S4), comprising an average of 55.5 tons of biomass (range: 28.5 to 83.6 tons, Figure 3 and Table S5). To put the abundance of high-flying *migrant hoverflies* in context, the estimate of 2.66 billion is ~10 times the mean annual numbers of silver Y moths *Autographa gamma* (285 million), and 70 times the number of painted lady butterflies *Vanessa cardui* involved in the largest migration event of recent years (37 million in 2009), which have been previously documented to migrate into and back out of the UK at high altitudes [41, 43]. If we assume that these aerial flows represent the density of adults on the ground in our southern British study region (surface area ~70,000 km^2), this equates to a mean of 38,000 km^{-2} (or 380 ha^{-1}) over the course of the year. The initial spring immigration is a comparatively small component of the annual total (accounting for just 20% on average), with a mean of 0.48 billion arriving each year (range: 0.29 to 0.74 billion, Table S4). The size of the subsequent 1–2 locally-produced generations, appearing from mid-summer onwards, was considerably larger than the initial spring invasion (mean: 4.5x larger, range: 1.3 to 8.1x larger, Table

S4), with a combined mean total of 2.18 billion detected flying overhead each year (range: 0.78 to 3.6 billion, Figure 3 and Table S4), split equally between mid-summer (42%) and autumn (38%).

The aerial bioflows of *migrant hoverflies* result in the spatial redistribution of large quantities of essential nutrients and energy over the southern British study region: during the course of the year, the ~30–80 tons of aerial biomass results in the long-range transport of 1000–2500 kg of N, 100–250 kg of P, and 50–150 GJ of energy (Table S5), which will be deposited considerable distances from their source. Due to the strong seasonal pattern of directional movement (Figure 2), much of this transport occurs towards the north during the spring immigration and towards the south during the autumn emigration. The southward-moving emigrants are considerably more abundant than the northward-moving colonisers in most years (mean: 2.5x larger, range: 0.5 to 5x larger, Figure 4 and Table S4). In most years (7 out of the 10 study years) southern Britain is a net exporter of *migrant hoverflies*, and their associated biomass, nutrients and energy content, to continental Europe. In an average year, ~0.5 billion more hoverflies (~12 tons of biomass) travel southwards towards the near-continent than arrive from there, with the net southward flow exceeding 1 billion hoverflies (mean biomass of ~28 tons) in 4 of the study years (Figure 4 and Table S4), a figure similar to that previously seen for the largest migrations of *A. gamma* observed in the same region [43].

Notwithstanding this considerable net transport of biomass, nutrients and energy, the biggest impact of the mass arrival of hoverflies each spring is via the provision of critical ecosystem services by the immigrants, and particularly their progeny. The mean number of aphids consumed by each larval *E. balteatus* under natural field conditions has been estimated to be 400 for larvae completing development [11]. We assume that the annual totals of VLR-detected *migrant hoverflies* from July onwards (i.e. the summer and autumn generations, mean annual total: 2.18 billion, Table S4) represents the total progeny surviving to adult-hood of the initial spring immigrants in each year (see STAR Methods). The larvae of these surviving hoverflies must have consumed an average of 0.871 trillion aphids per year (range: 0.3 to 1.5 trillion, Table S6) in order to complete development. However, each female of the initial spring influx is capable of producing ~400 eggs [44]; with an expected sex ratio of 1:1 among the immigrants, and an estimated 50% of immigrant females producing eggs, this leads to the second generation having an initial population size of 100x times the initial immigration (see STAR Methods). Our data suggests that only about 2% of this potential

population survive to adult-hood, but of the remaining hoverflies which perish before reaching the adult stage, a substantial proportion of them will have also consumed significant quantities of aphids before death. We have attempted to estimate the contribution these larvae make to aphid predation (see STAR Methods for our assumptions), and our calculations suggest that an additional mean of 5.44 trillion aphids per year (range: ~3 to 8 trillion, Table S6) will have been consumed by larvae which do not complete development. Thus the total aphid consumption of the progeny of the initial spring immigration is ~6.3 trillion aphids per year (~6,300 tons of aphid biomass), representing ~900,000 aphids ha^{-1} over southern Britain. In reality, the great majority of larval development will occur in lowland arable farmland where these species (particularly *E. balteatus*) are extremely important and abundant predators of cereal aphids [11, 37]. We therefore estimate that the contribution to pest aphid control is likely to be in excess of 1 million cereal aphids ha^{-1} of arable cropland, which is about 20% of typical aphid population densities in fields early in the season when hoverflies first appear (see STAR Methods for our assumptions).

In addition, species such as *E. balteatus* visit flowers in very high numbers [7–10, 34], and so they will also have important consequences for pollination services, via two processes. Firstly, the huge numbers mean they are one of the most frequent flower visitors, rivalling managed honeybees in numerical abundance during the summer (up to 4 billion *migrant hoverflies* in southern Britain during May–September, versus ~5 billion managed honeybees at peak abundance for the whole of Britain, see STAR Methods). Given that adult hoverflies (including *E. balteatus*) make hundreds of flower visits in their lifetime and are known to be efficient pollinators of both crops and wildflowers [8, 36], the pollination service provided by our focal species is clearly an important component of the total pollination provided by flower-visiting insects. Secondly, long-range migrants have the potential to successfully transport viable pollen between conspecific flowering plants over large spatial scales, which will lead to impacts on gene flow and population genetic structure [4, 5] if hoverflies routinely carry viable pollen during their journeys. To test this idea, we quantified pollen loads carried by actively migrating *E. balteatus* and *E. corollae* hoverflies (see STAR Methods). Average pollen loads were 10.5 grains per fly (range: 0–107) from up to 3 plant species (median: 2). These data suggest that the spring immigrants (~0.3–0.75 billion hoverflies) are capable of transporting ~3–8 billion pollen grains into southern Britain from the near-continent each year, while the equivalent values for

the autumn emigrants (~0.3–1.8 billion hoverflies) are ~3–19 billion pollen grains, with highly significant consequences for long-range gene flow mediated by insect migration.

Our results demonstrate that *migrant hoverflies* make enormous contributions to two crucial ecosystem services, namely biological control of pest aphids, and pollination of wildflowers and flowering crops. In addition, the huge numbers involved in the annual influx to higher latitudes will play important roles in nutrient and energy transfer, and provision of food to higher trophic levels such as larger predatory arthropods and insectivorous birds. Our data (Fig. 3) shows no discernible trend in abundance over the 10-year period, and this and other studies [7, 10, 34] indicate that migratory hoverflies (particularly *E. balteatus*) remain hugely abundant seasonal visitors to northern and central Europe with no sign of a recent decline in abundance; however, longer time-scales may be needed in order to detect declines in this group, so continued monitoring is crucial [10]. Considering that many other insect groups, especially pollinators, are undergoing alarming declines [7, 10, 13–19], our study indicates that migratory insects may play an increasingly important role in maintaining essential ecosystem services.

SUPPLEMENTAL INFORMATION

Supplemental Information includes 2 figures and 6 tables, and can be found with this article online at …

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AUTHOR CONTRIBUTIONS

J.W.C, K.R.W, G.H. and D.R.R. conceived the study. R.K.A.M, S.G.B. and M.H.M.M. provided crucial data, and K.S.L. provided crucial technical support for the radar work. B.G., G.H., K.R.W. and J.W.C. analysed the data. J.W.C., K.R.W. and B.G. wrote the first draft of the paper, and all authors made significant contributions to the final draft.

DECLARATION OF INTERESTS

The authors declare that they have no competing interests.

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Figure 1. Quantifying Hoverfly Migrations High above southern Britain

(A) High-flying *migrant hoverflies* were studied above a 70,000-km² region of southern Britain (black circle) using data from vertical-looking radars (VLR) at three locations (Malvern, Rothamsted and Chilbolton; red circles).

(B) Half-monthly numbers of VLR-detected hoverflies (black lines) show similar temporal patterns as the aggregated half-monthly counts of *Episyrphus balteatus* and *Eupeodes corollae* counted by the UK hoverfly recording scheme (HRS; blue lines); data is shown for every other year from 2000 to 2008, and the full dataset is shown in Figure S1.

(C) Correlation between half-monthly VLR-detected hoverflies and counts from the HRS for all data spanning 2000-2009 (Pearson's product moment correlation coefficient = 0.77, n = 100, $p < 0.001$).

(D) Vertical profile of total hoverfly abundance over the sampling range of the VLR; totals in the lowest three sampling altitudes have been corrected (blue components) to take account of target suppression due to inter-target interference (see STAR Methods and Figure S2).

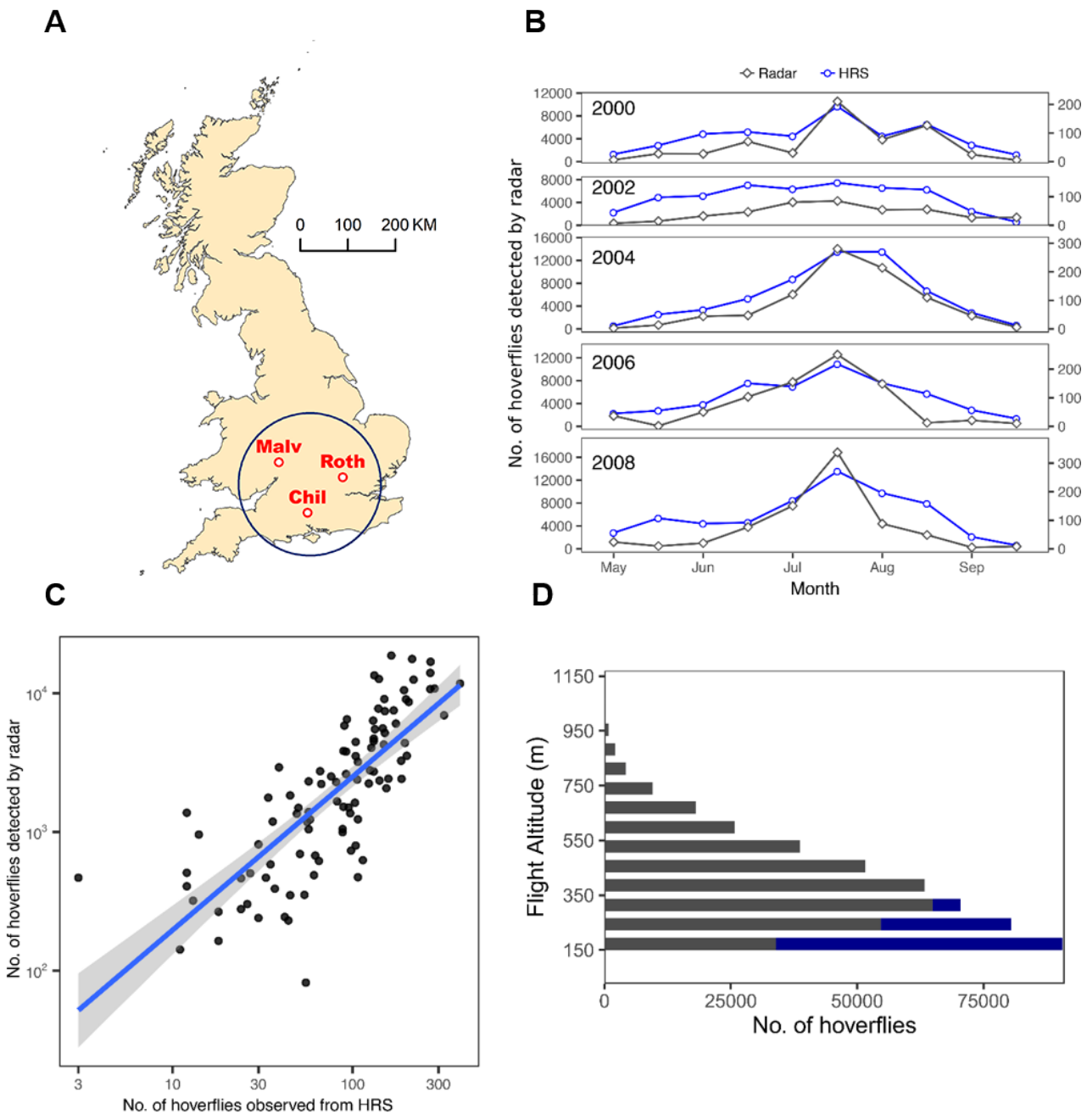

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Figure 2. Seasonally-beneficial Movement Directions

The circular plots show the windborne movement directions (tracks) of *migrant hoverflies* during mass migration events. The small circles on the periphery of the plots represent the mean direction of each individual mass migration. The bearing of the arrow indicates the overall mean direction in each half-monthly period, and arrow length represents the circular resultant length (r). Data are presented for each half-monthly period with enough migration events (>10) for circular analysis, and for the combined seasonal mean. See Table S3 for circular statistics for each half-monthly period.

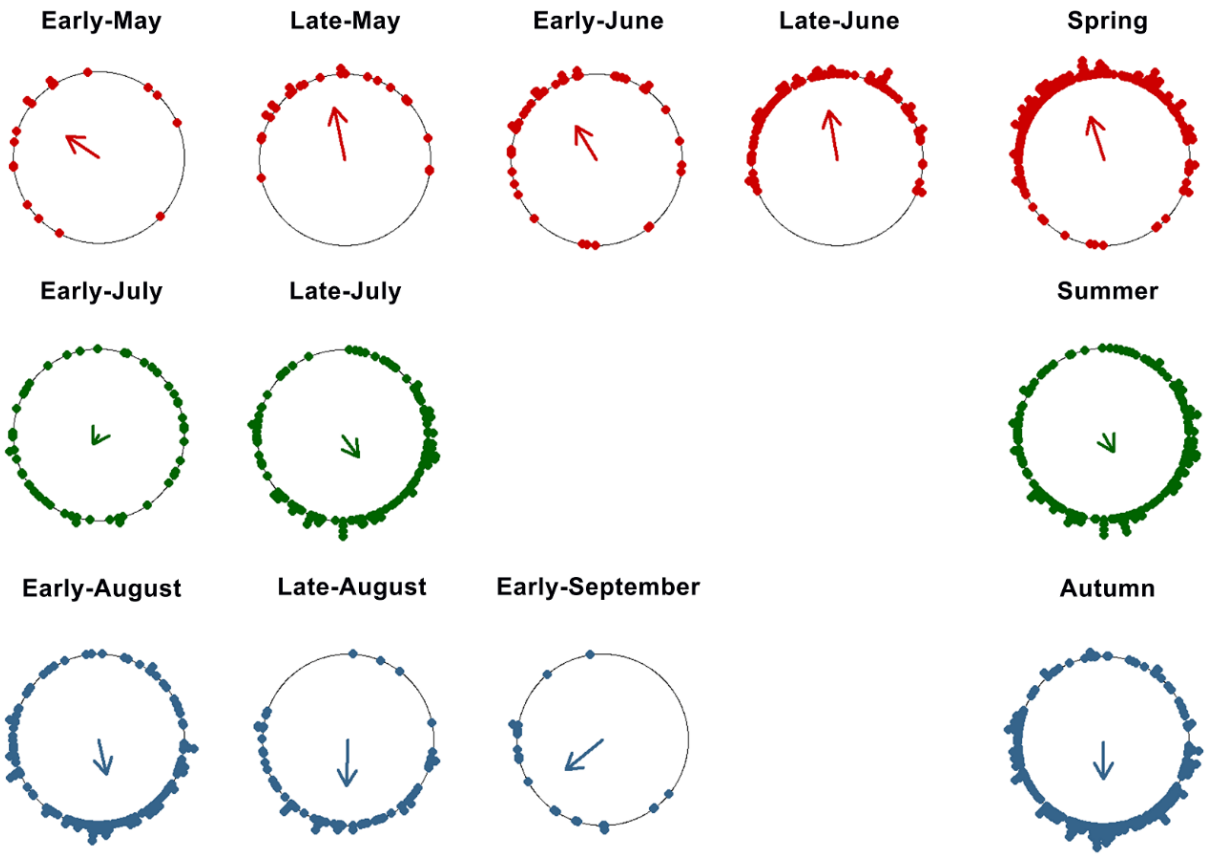


Figure 3. Seasonal and Annual Totals and Biomass

Lines represent the seasonal and annual total numbers of *migrant hoverflies* (in billions), and the wet biomass of these hoverflies (in tons), flying high above the study area. In the box plots, the solid lines represent medians, the dashed lines represents means, boxes represent interquartile ranges and whiskers extend to observations within 5% and 95% of the range. See Tables S4 and S5 for associated data.

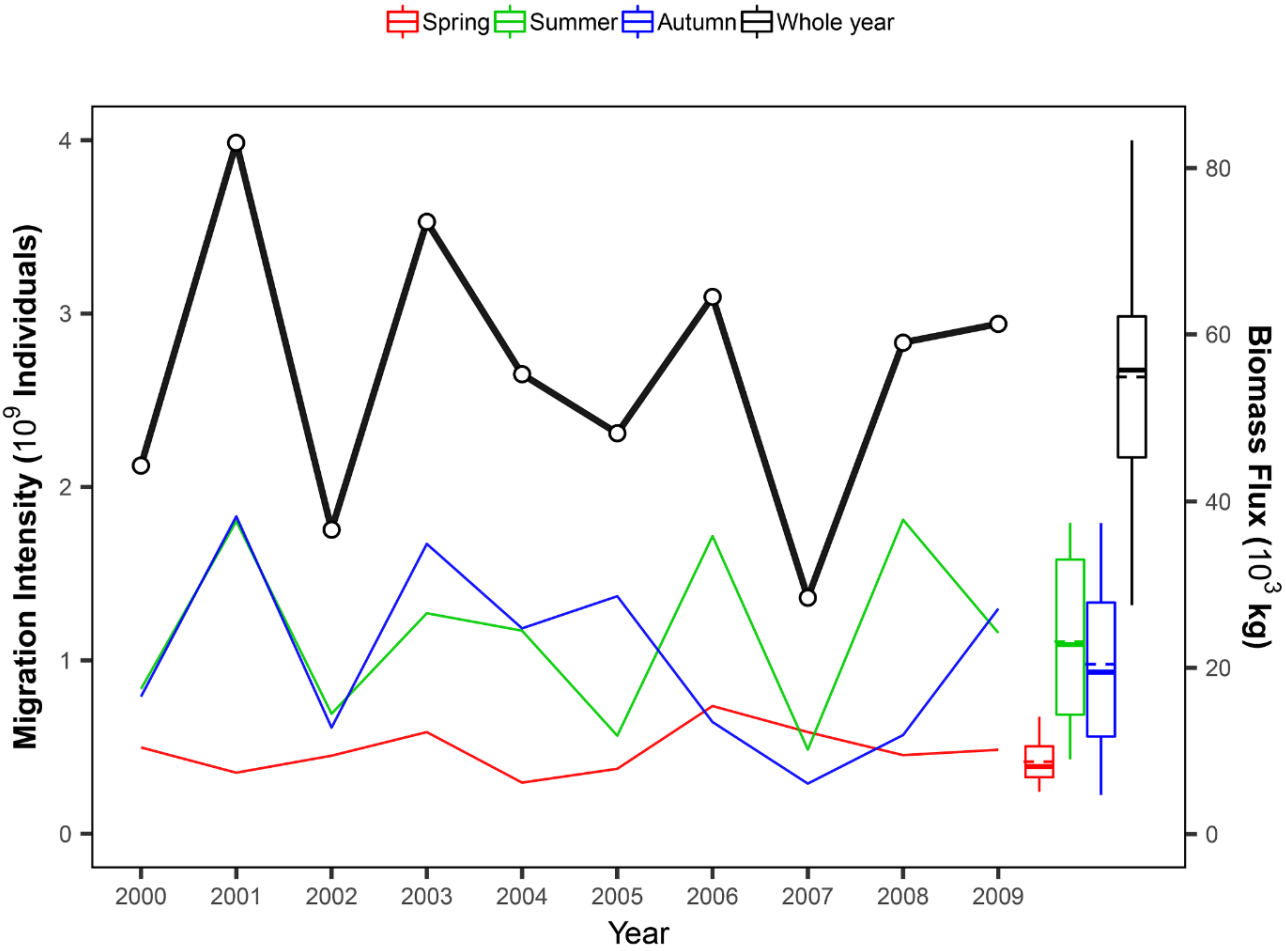
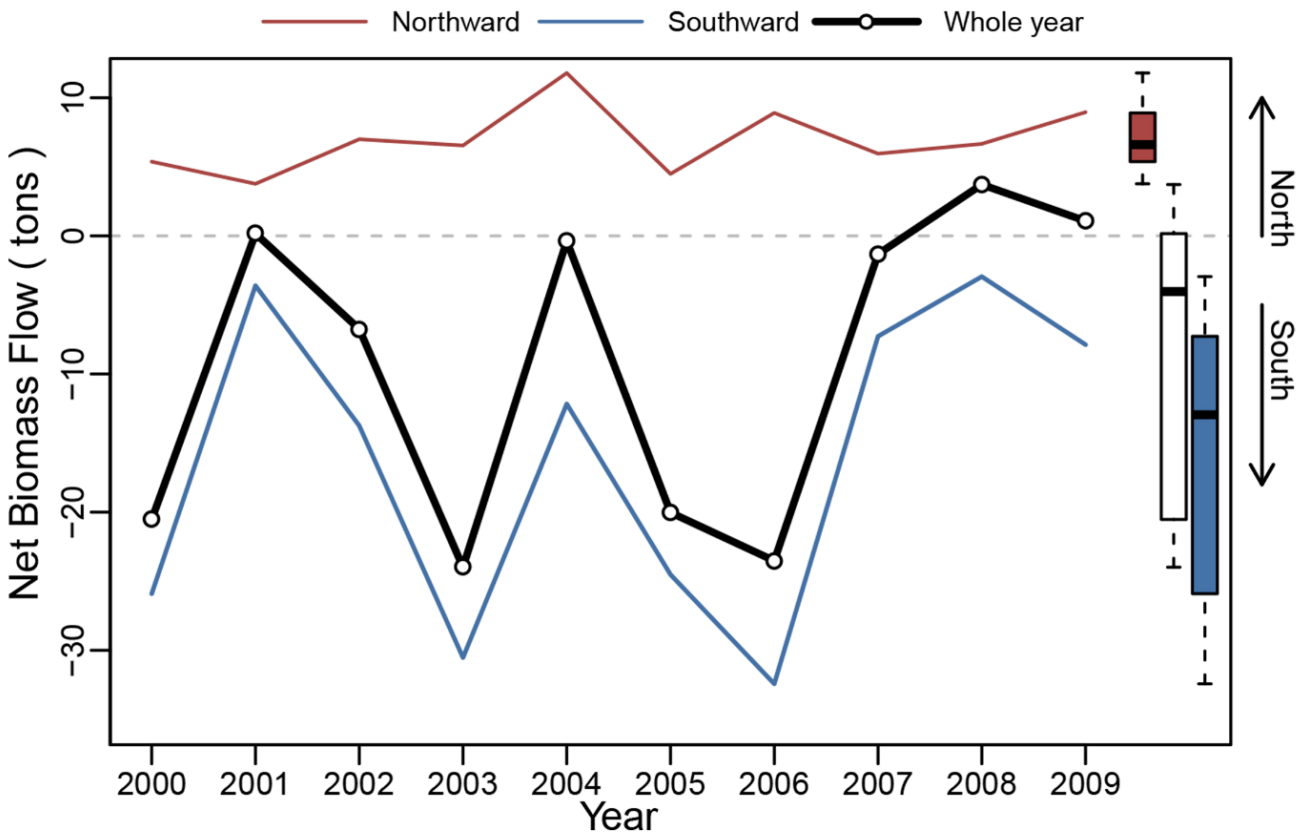


Figure 4. Net Biomass Flux of *Migrant Hoverflies* into and out of Southern Britain

The total wet biomass flow towards the north (red line) and towards the south (blue line) over the course of the year, and the combined net flow (black line) in each year. Negative values indicate a net southward movement, and positive values indicate a net northward movement. In the box plots, the solid lines represent medians, boxes represent interquartile ranges and whiskers extend to observations within 5% and 95% of the range. See Table S4 for associated data.



STAR METHODS

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Jason Chapman (j.chapman2@exeter.ac.uk).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We use remote sensing techniques to study natural high-altitude migrations of free-flying migratory hoverflies (Diptera; Syphidae), particularly the highly abundant species *Episyrphus balteatus* and *Eupeodes corollae* in the tribe Syrphini (collectively referred to as '*migrant hoverflies*' hereafter), above a large region of southern Britain during May to September of the 10-year period from 2000 to 2009 inclusive.

METHOD DETAILS

Radar Observations

We studied the migratory flights of hoverflies >150 m above ground level (agl) during daytime (defined as the period from 1 hour after sunrise until 1 hour before sunset) of the spring, summer and autumn of the 10-year period from 2000 until 2009 inclusive. We used data collected by purpose-built, vertical-looking entomological radars (VLRs) situated in southern England, as follows: Malvern, Worcestershire (lat. 52° 06' 04" N, long. 2° 18' 38" W) in south-western England from 2000 to 2003; Chilbolton, Hampshire (lat. 51° 8' 40" N, long. 1° 26' 13" W) in south-central England from 2004 to 2009; and Rothamsted, Harpenden, Hertfordshire (lat. 51° 48' 32" N, long. 0° 21' 27" W) in south-eastern England from 2000 to 2009. The VLR equipment and operating procedures are described in detail elsewhere [12, 26]. Briefly, the radars provide a range of information – including body mass, flight altitude (insects are detected within 15 separate altitude bands), aerial density, displacement speed, displacement direction, and flight heading – for all individual insects of >2 mg body mass that fly through the vertically-pointing 3.2 cm wavelength (X-band) beam within the altitude range of 150–1200 m agl. The VLRs record the total migration intensity of specific classes of targets selected for further study (migratory hoverflies in this case) throughout the sensed volume of the atmosphere above the radar, and this sensed volume is precisely known for all possible insect body masses [45]. Thus we were able to accurately quantify the total migration intensity of hoverflies through the study

region (in terms of numbers of individuals) and the total biomass of this population (see below for description of the methods).

In order to define the spring, summer and autumn periods, we plotted migratory track directions of the hoverflies on a half-monthly basis (Figure 2, Table S3). There was a clear seasonal pattern, with seasonally-beneficial movements towards the north in May and June, followed by a period with no overall direction during July, and then seasonally-beneficial movements once again in August and September but this time directed southwards (Figure 2, Table S3). Radar data for the months preceding and following the May–September migration period were far too sparse for analysis, and so were excluded from further consideration. We therefore defined the spring immigration period as May and June, the mid-summer dispersal period as July, and the autumn emigration period as August and September, similar to the observed pattern of seasonal movement directions in previous analyses of high-altitude insect migration [3, 24, 39, 46].

The three radar locations are approximately 100–120 km apart, and preliminary observation of the data in the current study, and previous analyses of diurnal data [3], indicate that the aerial densities, migration directions, movement speeds, flight altitudes and taxonomic diversity measured at each site were very similar. We therefore combined our data from the 3 radar locations for the purposes of analysis, and we assumed that the data collected at each location was representative over distances of up to at least 120 km away from each site. We defined our study region as the volume of atmosphere between 150–1200 m agl, above an area delimited by a circle of 300 km diameter (Figure 1A), which had a surface area of 70,686 km^2. The height range of 150–1200 m was primarily selected as this is the sampling range of the VLRs and we therefore have the most reliable data from this height range. In Britain, there will be extremely limited migration above the 1200 m ceiling as it is generally too cold above this height for insect flight [26], and examination of the VLR-measured vertical profiles of hoverfly density (Figure 1D) indicates that densities decline with increasing altitude to zero in the highest sampling band of the VLR just below 1200 m. Below 150 m, hoverflies densities may well be much higher; however, these lower-flying hoverflies will not be involved in the long-range seasonal movements we are concerned with in this paper, and therefore we excluded them from our analyses. Our reasoning for this is that larger insect migrants climb at speeds of 0.5–2.5 m/s when initiating migratory flights [26]; thus migrating hoverflies will rise above 100 m in just a few minutes of climbing flight. Given that we are concerned with long-range exchanges of biomass and nutrients in this study, we therefore decided to exclude hoverflies flying below the VLR lowest sampling height of 150 m agl, as the short flights which occur at low altitudes will be unimportant in terms of seasonal long-range transport.

Selection of hoverfly radar data

Historical field observations of concentrated insect migration through mountain passes in the Pyrenees by David and Elizabeth Lack in the 1950s [27] and in the Swiss Alps by Jacques Aubert and colleagues [29, 30] during the 60s and 70s (Table S1), plus recent observations in the Swiss

Alps and the Pyrenees (unpublished data from M.H.M.M. and K.R.W., respectively), have established that migratory hoverflies are hugely abundant insect migrants during the autumn migration period, with counts of hoverflies passing through a pass often exceeding tens of thousands of individuals per day. Although there are no similar systematic observations from Britain, mass arrivals of migratory hoverflies have also been frequently documented around Britain over the past century [28], and they have been recorded over the North Sea far from land [47]. We therefore assumed that hoverflies may be migrating into and back out of southern Britain in large numbers, and decided to make them the subject of this study. A range of species have been recorded as taking part in these migrations, but by far the most abundant component of the migrations through Alpine passes is the marmalade hoverfly *Episyrphus balteatus* (Table S1), a member of the subfamily Syrphinae and tribe Syrphini. This species is the commonest hoverfly in Britain and the spring populations (which appear in May and June) are believed to result almost entirely from immigration from southern Europe [48]. Extensive aerial netting samples collected at heights of around 200 m agl during the spring, summer and autumn periods of the years 1999 to 2007 at a site in central Bedfordshire (Cardington airfield) [49], just 35 km to the north of the Rothamsted VLR, reveal that *Episyrphus balteatus* is the most frequent hoverfly caught migrating at altitude in southern Britain (Table S2). We therefore decided to focus on this species for our study of hoverfly migration. [It will be noted (Table S1) that *Eristalis tenax* (the drone fly) is also a common syrphid migrant in central Europe. However, this species is not an obligate migrant in UK – being present over the winter – and, furthermore, the larvae are not aphidophagous. So, after consideration, we decided to omit this species from our analyses. As it is considerably larger than *E. balteatus* (Table S1), this was straightforward to achieve.]

We selected radar targets that we believed to be produced by migrating *Episyrphus balteatus* (and other abundant '*migrant hoverflies*' in the Syrphini with similar physical characteristics) by the following method. Firstly we used body-mass data provided by Francis Gilbert to characterise the mass range of *Episyrphus balteatus* as 22.3 mg ± 6.6 mg (mean ± 1 standard deviation, n = 18, Table S1), and then used these figures to filter the radar data to match our study species by restricting our analyses to a mass range of 15–28 mg. To further filter our data so that the selected targets were restricted to hoverflies, we next used radar reflectivity values [26, 38] to select targets with the expected body shape criteria of *Episyrphus balteatus*. We measured the two principal ventral aspect radar cross sections (RCS), namely the parallel RCS (σ_{xx}) and the transverse body axis (σ_{yy}), of wild-caught *Episyrphus balteatus* (Table S2) using our X-band linear polarisation transmission rig in our laboratory at Rothamsted [37]. These laboratory measurements indicated that *Episyrphus balteatus* has values of σ_{xx} / σ_{yy} of 8.8 ± 4.0 (mean ± 1 standard deviation, n = 7, Table S2), and so we selected radar targets with values of σ_{xx} / σ_{yy} of between 5–10 as these fell entirely within the range of our laboratory measured individuals. Body-mass data for other migratory hoverflies presented in Table S1 show that the majority of species can be ruled out based on body-mass alone, and that only *Eupeodes corollae* overlaps with *Episyrphus balteatus*. Data from the studies of

578 migration through the mountain passes (Table S1), and its presence in aerial captures above
579 southern Britain (Table S2), confirm that a significant proportion of *Eupeodes corollae* are expected
580 to be included in our radar dataset. We therefore consider that our radar data on '*migrant hoverflies*'
581 will have been largely produced by these two numerous species, and the majority of the data
582 produced solely by *Episyrphus balteatus*.
583 Examination of our aerial samples of thousands of high-flying insects caught above southern
584 Britain [49] indicates that the only other abundant day-flying migrants in the same size category as
585 our selected *migrant hoverflies* (15–28 mg) are 7-spot and harlequin ladybird beetles (*Coccinella*
586 *septempunctata* and *Harmonia axyridis*, respectively [49, 50]). However, ladybirds have very
587 different RCS values to hoverflies, with values of σ_{xx} / σ_{yy} of 1–3 [50], and so they can be easily
588 excluded. We are therefore confident that our selected radar targets are indeed produced by *migrant*
589 *hoverflies*, predominantly *Episyrphus balteatus* and *Eupeodes corollae*.
590 A hoverfly 'migration occasion' was defined as any occasion when at least 1 '*migrant hoverfly*'
591 was detected in the daytime period by one of the radars between 150–1200 m agl; this resulted in
592 2,628 occasions (containing 367,817 individual radar targets) being available for analysis (Table S3).
593 This dataset was used to calculate the seasonal and annual patterns of hoverfly migration intensity
594 and biomass flux (see below). To analyse directional patterns (see below), we used a subset of the
595 data which we termed hoverfly 'mass migrations'. These were selected by: (1) ordering all days in
596 each season from the highest number of hoverflies detected to the lowest; (2) selecting all migration
597 occasions as migration events until cumulatively 75% of the total number of individual hoverflies in
598 that season was reached; and (3) all remaining days with hoverflies were excluded from the
599 directional analyses. This ensures that only days of major migration are used to identify seasonal
600 migration patterns. This process resulted in 615 of the hoverfly migration occasions (23% of the total
601 occasions, involving 273,247 individual hoverflies) being defined as mass migrations (Table S3).
602
603
604 ## QUANTIFICATION AND STATISTICAL ANALYSIS
605
606 ### Seasonal migration directions (Figure 2)
607 For each individual insect that passes through the beam, the VLR automatically records the
608 migratory track (i.e. the displacement direction, which is largely determined by the wind but which is
609 also influenced somewhat by the insect's flight vector) [12, 26, 45, 51]. The mean track (i.e. the
610 migration direction), plus associated circular statistics, were calculated for all 'mass migrations' of
611 hoverflies (Table S3) during all three seasons (spring, summer and autumn) in the years 2000–2009.
612 For each mass migration, the following two parameters were calculated for the distributions of
613 individual tracks: (i) the mean direction; and (ii) the mean circular resultant length 'r' (a measure of
614 the clustering of the angular distribution of headings or displacements ranging from 0 to 1, with higher
615 values indicating tighter clustering around the mean). Rayleigh's test of uniformity [52] was then used

to test the null hypothesis that the distributions of tracks fitted a uniform distribution (an observed *P*-value of <0.05 indicates that the distribution is significantly unimodal, and hence the individual insects in that mass migration show a significant degree of common alignment of their tracks). All hoverfly migration events had unimodal distributions of tracks, reflecting the fact that they are strongly influenced by the wind which, during fair weather, is not expected to change its direction by any great degree over the course of the day.

We then calculated the overall mean track for each half-monthly period and for each season, by analysing the individual mean values from all hoverfly mass migrations in each period with the Rayleigh test once again (Figure 2 and Table S3). If the overall distribution of mean tracks was also significantly unimodal, we assumed that there was a preferred migration direction during this period; whereas if the distribution did not differ significantly from a uniform distribution, we assumed that there was no preferred migration direction during that period.

In addition, we compared seasonal migration directions and associated statistics for the spring and autumn seasons in the first three sampling altitudes of the radar (range gates 1–3, between 150 m and 350 m) with those from the second three sampling altitudes (range gates 4–6, between 350 m and 550 m, see Figure 1D). This comparison was conducted to test whether flight altitude had any effect on the 'directedness' of the hoverfly movements, which might indicate an increase in the proportion of migrants with altitude. The spring values for gates 1–3 (Rayleigh test, migration direction = 325°, n = 59, r = 0.54, $p < 0.0001$) and for gates 4–6 (349°, n = 125, r = 0.53, $p < 0.0001$) had similar directions, but crucially the Rayleigh test 'r-values' were essentially identical, indicating that the lower-flying hoverflies were just as directed as the higher-flying ones. Exactly the same pattern occurred in the autumn, where values for gates 1–3 (169°, n = 56, r = 0.43, $p < 0.0001$) and for gates 4–6 (185°, n = 188, r = 0.43, $p < 0.0001$) once again had similar directions but identical 'r-values'. We therefore conclude from this that all the hoverflies flying within the detection range of the VLRs were engaged in long-range migration.

Migration intensity and biomass (Figure 3)

We calculated an aerial density value (per 10^7 m^3) for each individual migrant hoverfly detected by the 3 radars during the study period (daytime of the spring, summer and autumn of each year during 2000–2009), based upon the volume of atmosphere sensed by the VLR and the displacement speed of each individual insect [45]. The total aerial density of *migrant hoverflies* above each radar site during the spring, summer and autumn migration seasons in each of the 10 years was calculated in the following manner. Firstly, we calculated the combined aerial density of all hoverflies detected in each of the VLR's 15 altitude bands, and plotted the mean values in each altitude band over the study period (the dark grey bars in Figure 1D). The lowest altitude bands showed reduced densities of hoverflies (Figure 1D), due to high levels of multiple-target interference caused by two or more insects passing through the beam in the same altitude band and at the same time [26], a phenomenon routinely experienced in the lowest gates during intense daytime migrations [45]. We

corrected for this underestimation of true hoverfly aerial density in the first three altitude bands by fitting a log-linear regression to the observed aerial density values of *migrant hoverflies* in altitude bands 10 down to 4, and then extrapolating this to produce expected aerial densities in altitude bands 1 to 3 (Figure S2). This produced estimated aerial densities that were 2.667, 1.472 and 1.086 times the observed values in altitude bands 1, 2 and 3 respectively (Figure S2). These corrected values were used to plot the true density-height relationship of *migrant hoverflies*, and the additional density that was added by this process is shown by the blue component of the horizontal bars in Figure 1D.

Next we summed the aerial-density values of the hoverflies in each gate during each 5-minute time period, and then divided this value by the number of radar-sampling periods (~56 during the daytime), and then by 15 (the number of altitude-bands). This value (*X*) is equal to the total aerial density of hoverflies per 10^7 m³ on each day within the air column above each radar site. We converted these aerial-density values to a daily migration flow through a 1-km by 1-km (10^6 m²) 'window' above the radar, running west to east (and thus parallel to the principal migration directions during the spring and autumn; Figure 2 and Table S3). This was achieved by the following procedure. Firstly, the migration flow through the 1-km² window each second (*Y*) was calculated by: *Y* (km^{-2} s^{-1}) = (*X*/10) x mean displacement speed (m s^{-1}). Secondly, the total migration flow through the 1-km² window over the daytime (*Z*) was calculated by: *Z* (km^{-2} day^{-1}) = *Y* x *N* seconds, where *N* is the number of seconds in the daytime study period. The total migration flow values km^{-2} day^{-1} (*Z*) were used to calculate the mean daily migration flow of hoverflies during the whole of the spring, summer and autumn migration seasons, for each year and across all radar sites. To calculate the total seasonal movement over the ~70,000 km^2 study area (see Figure 1A), we extrapolated from the daily flow rates above each radar site to produce an estimate of the numbers crossing a line running west to east (i.e. perpendicular to the main migration direction which is north–south) along a 300-km stretch of southern Britain (Figure 3 and Table S4). Using the individual body masses measured by the VLRs for every single *migrant hoverfly*, the migration intensities were then converted to biomass flux (Figure 3 and Table S5).

Net flux of biomass and energy (Figure 4)

We calculated of net flows of biomass to the north and to the south for all *migrant hoverflies* recorded across the entire flight season (Figure 4). The total biomass moving towards the north (defined as migratory tracks between 270° clockwise through 0° to 90°) was assigned a positive value, while the total biomass moving towards the south (defined as migratory tracks between 90° clockwise through 180° to 270°) was assigned a negative value. The sum of these daily values across the entire year produced the annual net flow of biomass towards the north or south (Figure 4 and Table S4).

We calculated the total amounts of nitrogen (N) and phosphorus (P) in the annual hoverfly movements in the following way. Based on the results of Finke [53] for house crickets *Acheta domesticus*, we assumed hoverflies are composed of 69.2% water and 30.8% dry matter; thus, the

692 mean annual value of 55.53 tons of migrant hoverfly wet biomass (Table S5) represented 17.1 tons
693 of dry matter. Insects are typically composed of 10% N by dry weight, and 1% P by dry weight, and
694 thus the aerial movements involve an annual average of 1,710 kg N and 171 kg P (Table S5).
695 Based on data from Finke [53] for house crickets *A. domesticus*, we presumed that each kg of
696 the dry mass of the *migrant hoverflies* contained 1402 kilocalories, which is equivalent to 5.87 million
697 Joules per kg. For the mean annual value of 55.53 tons of hoverfly dry mass migrating above
698 southern Britain, this equates to 100 GigaJoules (Table S5).
699
700 **Quantification of ecosystem services**
701 We estimated the contribution that *migrant hoverflies* make to natural biological control of pest aphids
702 by quantifying the total number of aphids which would have been eaten by the progeny of the initial
703 immigrants in every year, and then making the assumption that the great majority of these aphids
704 would be pest cereal aphids as these are the most abundant aphid species in Britain by far [49]. We
705 used the annual estimates of *migrant hoverflies* detected during the summer and autumn seasons
706 as a measure of the total progeny surviving to adult-hood from the initial spring immigration in each
707 year (annual mean equals 2.18 billion hoverflies, Table S4). Based on the estimate that under natural
708 field conditions, each larval *Episyrphus balteatus* will consume 400 aphids during its entire larval
709 development period [11], this produces a mean annual value of 0.871 trillion aphids consumed by
710 the surviving progeny (Table S6). However, the larvae survive into adult-hood will only be a tiny
711 proportion of the total larvae produced by the initial spring immigration, and so we also estimate the
712 aphid consumption by the larval component which did not survive. We assume that 50% of the initial
713 spring immigration (annual mean = 0.48 billion hoverflies, Table S4) will be female, and additionally
714 we assume that only 50% of those females will arrive safely, find a mate and produce fertile eggs
715 (that is, an annual mean of 0.12 billion hoverflies will produce eggs). Mean fecundity of these females
716 is assumed to be 400 eggs [44], and so the annual mean number of eggs produced will be 100x
717 greater than the size of the initial spring immigration (annual mean = 48 billion eggs produced).
718 Based on lab studies of development rates of larval *Episyrphus balteatus*, and daily consumption
719 rates of aphids by the larvae, carried out by Jalilian [54], we make the following assumptions in our
720 calculations: (i) that larvae live for 10 days (3 days as 1st instar, 3 days as 2nd instar, and 4 days as
721 3rd instar [54]); (ii) that they consume 8 aphids per day in the 1st instar, 37 aphids per day in the 2nd
722 instar, and 64 aphids per day in the 3rd instar [54]; and (iii) that 10% of all larvae die on each day of
723 development. Using this method, we calculated the total aphid consumption from the proportion of
724 hoverfly larvae produced by the initial spring immigration which did not survive to adulthood for each
725 year (mean annual value = 5.44 trillion aphids, Table S6). When added to the number consumed by
726 larvae surviving to adulthood, this produced a mean value of 6.31 trillion aphids (range: 4.22 – 9.31
727 trillion, Table S6). The mean total value of aphids consumed for the whole of southern Britain was
728 converted to the number of aphids per hectare, by dividing by the total number of ha in the study
729 region (70,000 km^2 x 100 ha = 7 million hectares) to give a value of 6.31 trillion / 7 million = 900,000

aphids per ha. As most hoverfly development will occur in agricultural land, we use 1 million aphids per ha as a conservative value for the predation of pest aphids exerted by *migrant hoverflies*. Initial population densities of cereal aphids on winter wheat during the early part of the season (when hoverfly larvae first appear in the crop) are typically around 500 aphids per m^2 [55, 56], which corresponds to a value of 5 million aphids per ha. Our estimate of aphid predation from *migrant hoverflie*s is therefore about 20% of the initial population density.

For the discussion of the role that *migrant hoverflies* play in pollination services, we compared them to honeybees. We estimated the managed honeybee population for Britain using the following information. Firstly, the National Bee Unit's 'Hive Count' project (http://www.nationalbeeunit.com/index.cfm?pageid=362) estimates that there were 247,000 managed honeybee hives in Britain in 2017. The British Beekeeping Association's newsletter 'Life in the hive' (accessed through a beekeeping blog available at: https://adventuresinbeeland.com/2018/01/05/how-many-honey-bees-are-there/) states that British honeybee hives range from 5,000 to 35,000 worker bees, so we assume a mean value of 20,000 worker bees per hive. These estimates give a value of 4.94 billion worker honeybees in Britain during 2017.

To estimate the quantity of pollen transported by hoverflies immigrating into, and emigrating out of, southern Britain, actively migrating *E. balteatus* and *E. corollae* were collected on autumn migration through the col de Bretolet in the Swiss Alps during September and October 2018 to assess average pollen loads. 30 hoverflies (27 *E. corollae* and 3 *E. balteatus*) were collected in an interception trap during their migration through the narrow, high-altitude pass, and killed with ethyl acetate. The pinned specimens were swabbed for pollen in May 2019 using small (3 mm^3) cubes of fuchsin gel [57]. The cubes were then melted onto a microscope slide and all pollen grains counted using a binocular microscope. As these collected hoverflies were actively migrating at the time, we assume that hoverflies migrating into Britain will carry similar pollen loads, as they will frequently feed at flowers before and during migration in order to build up fuel loads for flight. As pollen carried by actively migrating insects can stay viable for up to 2 days [4, 58], *migrant hoverflies* crossing the English Channel between southern Britain and Europe will be very capable of transporting viable pollen distances of hundreds of kilometres between these two regions.

DATA AND SOFTWARE AVAILABILITY

The raw radar data from this study have been deposited in the Mendeley Data repository (http://dx.doi.org/10.17632/ysrgpm379b.1).

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Vertical-looking Radar data of migrant hoverflies	This paper	http://dx.doi.org/10.17632/ysrgpm379b.1

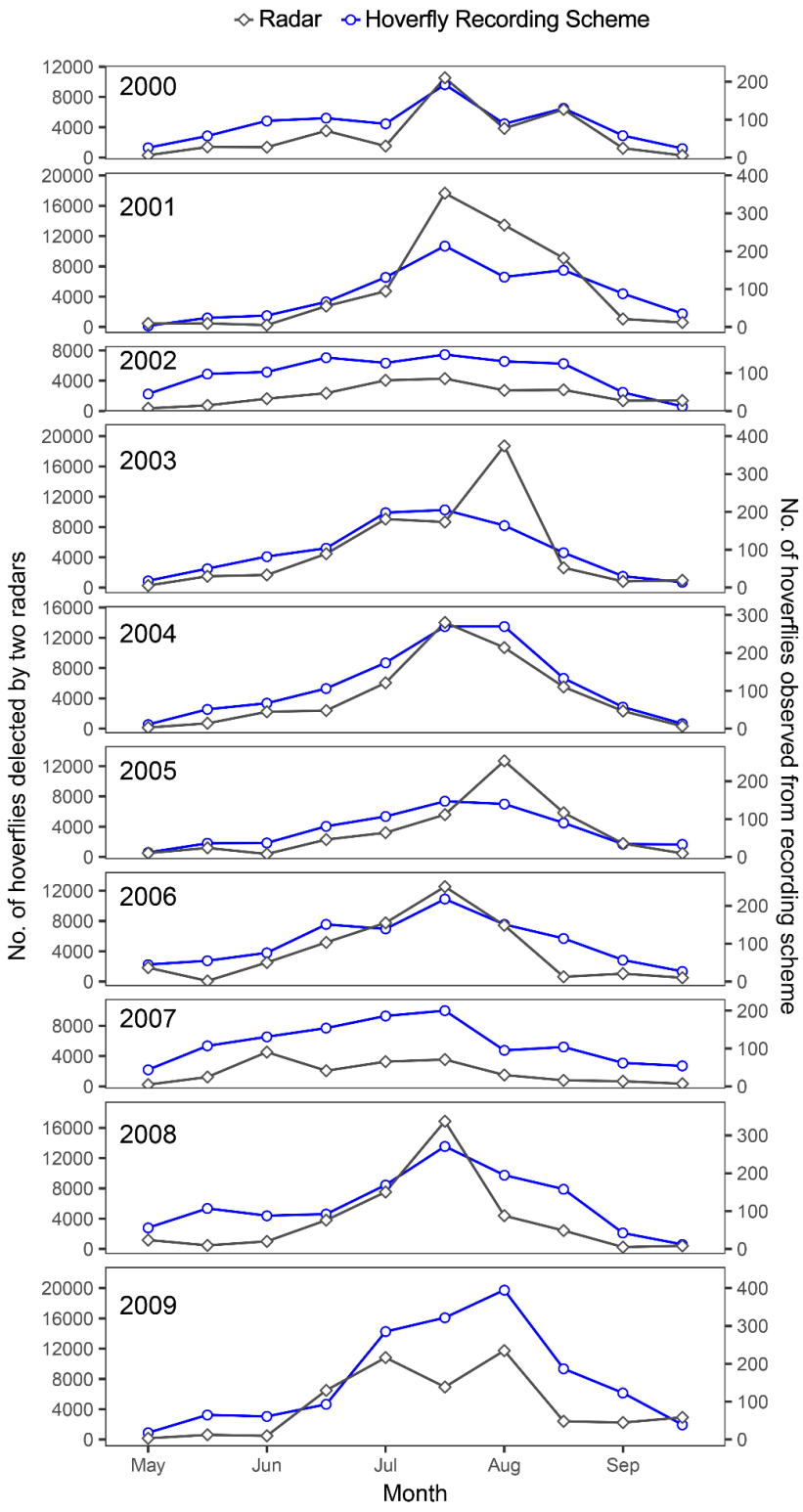


Figure S1. Confirmation that radar-detected *migrant hoverflies* were correctly classified

Related to Figures 1B and 1C. Half-monthly numbers of VLR-detected *migrant hoverflies* (black lines) and the aggregated half-monthly counts of *Episyrphus balteatus* and *Eupeodes corollae* from the UK hoverfly recording scheme (HRS; blue lines). A subset of this data is presented in Fig. 1B of the main paper, and the result of the correlation of these datasets is shown in Fig. 1C of the main paper.

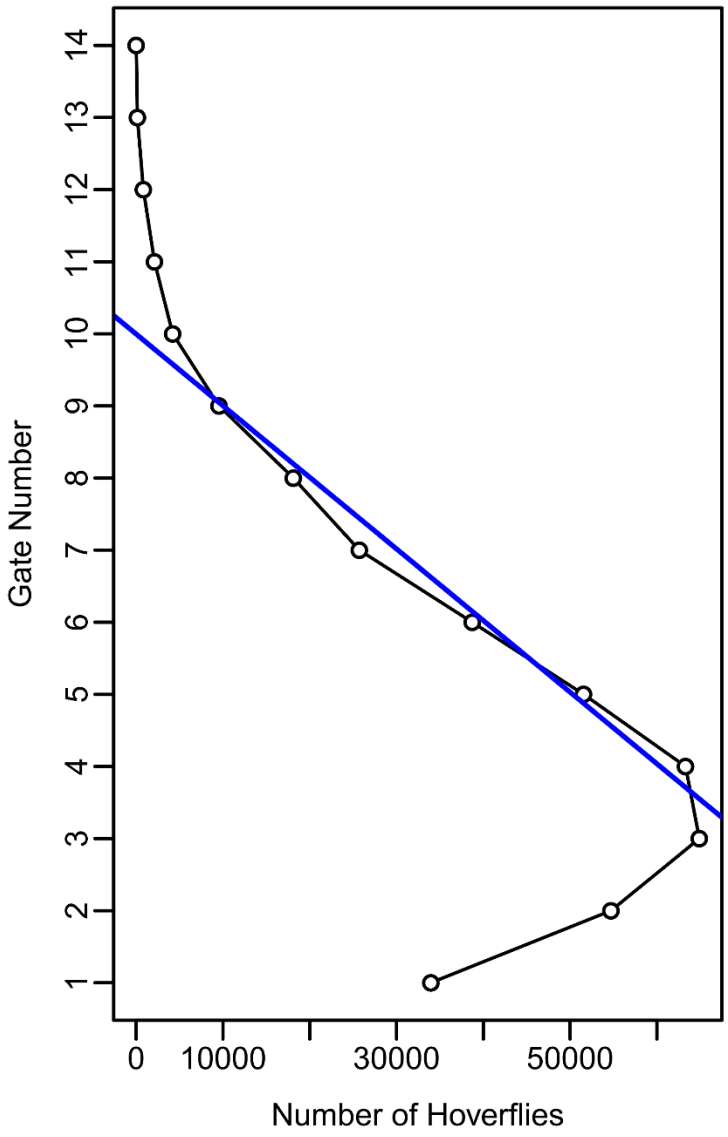


Figure S2. Corrected altitude profile of *migrant hoverflies*

Related to Figure 1D. Density-height relationship for VLR-detected *migrant hoverflies* (black line and open circles), and the log-linear regression (blue line) based on data in altitude bands 10 down to 4. This relationship was then extrapolated for altitude bands 3 down to 1, in order to estimate the actual density values in altitude bands 1 to 3. These values were used to correct the observed values in the lower three altitude bands (see the blue portions of the density values in Fig. 1D in the main paper).

Sub-family and Tribe	Species	Proportion of all migrant Syrphids (%)	Weight (mg)	SD	n
Syrphinae					
Bacchini	*Melanostoma mellinum*	1.32% (N = 31,573)	6.4	3.6	11
Syrphini	*Sphaerophoria scripta*	6.10% (N = 146,210)	10.9	2.7	4
	Episyrphus balteatus	52.77% (N = 1,264,568)	22.3	6.6	18
	Eupeodes corollae	6.71% (N = 160,685)	21.4	7.7	21
	Syrphus ribesii	2.80%* (N = 67,121)	34.9	8.9	69
	Scaeva pyrastri	0.47% (N = 11,168)	32.8	-	1
Eristalinae					
Eristalini	*Eristalis tenax*	26.51% (N = 635,294)	110.2	35.3	23
	Helophilus trivittatus	0.08% (N = 1,988)	30.0	-	1

Table S1. Migratory hoverfly abundances and body masses

Related to Figures 1B and 1C. Abundances were calculated by Aubert et al. [S1] from captures of over 2 million Syrphids migrating through the Col de Bretolet in the Swiss Alps during the autumns of 1962 to 1973. The two species which are the focus of this study are highlighted in bold. All body mass data was recorded by Professor Francis Gilbert from hoverflies captured in England and kindly shared for this study. Abbreviations are F for female, M for male, and SD for standard deviation.

*All *Syrphus* species included in counts

Date	Time of day	Wind speed (m/s)	Species	Number	Density (number per 10^5 m^3) ‡
16-Jul-99	13:45 - 18:55	9.4	*Episyrphus balteatus*	1	0.89
20-Jul-04	10:10 - 14:20	6.1	*E. balteatus*	2	3.4
23-Jul-04	09:35 - 14:00	7.2	*E. balteatus*	1	1.4
20-Jul-04	10:10 - 14:20	6.1	*Eupeodes corollae*	1	1.7
07-Jul-07	11:30 - 14:10	9.2	*Melanostoma mellinum*	1	1.8

Individual	σ_{xx} (cm^2)	σ_{yy} (cm^2)	Ratio (xx/yy)
E. balteatus #1	0.0640	0.0068	9.41
E. balteatus #2	0.1100	0.0068	16.18
E. balteatus #3	0.1200	0.0180	6.67
E. balteatus #4	0.0600	0.0120	5.00
E. balteatus #5	0.0700	0.0120	5.83
E. balteatus #6	0.0600	0.0090	6.67
E. balteatus #7	0.0300	0.0025	12.00
Mean	0.0734	0.0096	8.8221
1 S.D.	0.0312	0.0050	4.03

Table S2. Syrphids caught by aerial sampling at ~ 200 m above ground at Cardington Airfield, Bedfordshire, England*, and radar cross-section measurements[$] for wild-caught *Episyrphus balteatus*

Related to Figures 1B and 1C.

* For sampling methods see Chapman et al. [S2]

[$] For further details see Drake et al. [S3]

‡ Note: these densities are thought to be minimal, as hoverflies were only caught under rather windy conditions. In lower wind speeds at the sampling height, the flies may well be able to avoid the net entrance. This can certainly happen with nets in alpine passes in winds below ~5 m/s (M.H.M. Menz, personal observations).

Season		Number of Migration Occasions		Number of Insects		Migratory Track (Windborne Displacement Direction)			
	Half-monthly Period	All	Mass Migration Events	All	Mass Migration Events	n (Migration Events)	Direction (°)	r	p
Spring (Immigration)	Early-May	197	17 (8.63%)	5,010	2,712 (54.13%)	17	303.25	0.45	0.0319
	Late-May	220	25 (11.36%)	7,549	3,951 (52.34%)	25	348.28	0.62	<0.0001
	Early-June	228	45 (19.74%)	14,054	9,626 (68.49%)	45	327.78	0.46	<0.0001
	Late-June	286	99 (34.62%)	36,141	30,813 (85.26%)	99	349.72	0.58	<0.0001
	Total	**931**	**186 (19.98%)**	**62,754**	**46,562 (74.20%)**	**186**	**341.75**	**0.53**	**<0.0001**
Mid-summer (Dispersal)	Early-July	271	52 (19.19%)	49,922	33,062 (66.28%)	52	---	0.13	0.4164
	Late-July	327	129 (39.45%)	108,597	84,647 (77.95%)	129	142.78	0.31	<0.0001
	Total	**598**	**181 (30.27%)**	**158,519**	**117,709 (74.26%)**	**181**	**151.16**	**0.24**	**<0.0001**
Autumn (Emigration)	Early-Aug	275	146 (53.09%)	84,675	75,263 (88.88%)	146	167.38	0.41	<0.0001
	Late-Aug	311	71 (22.83%)	40,953	28,414 (69.38%)	71	181.98	0.54	<0.0001
	Early-Sept	245	21 (8.57%)	12,312	3,435 (27.90%)	21	230.88	0.56	0.0007
	Late-Sept	268	10 (3.73%)	8,604	1,864 (21.66%)	10	---	0.25	0.5464
	Total	**1,099**	**248 (22.57%)**	**146,544**	**108,976 (74.36%)**	**248**	**179.87**	**0.43**	**<0.0001**
Whole Year	**Grand Total**	**2,628**	**615 (23.40%)**	**367,817**	**273,247 (74.29%)**				

Table S3. Total number of migration occasions, number of 'mass migrations events', number of individual insects detected, and half-monthly migratory track directions of *migrant hoverflies* flying high above southern Britain

Related to Figure 2. Seasons are colour-coded to correspond with colours used in Figures 2, 3 and 4 in the main paper.

	Total number (billions) of *migrant hoverflies* in each season					Total number (billions)			Total biomass (tons)		
Year	Spring	Mid-summer	Autumn	Progeny	**Annual Total**	**North-ward**	**South-ward**	**Net**	**North-ward**	**South-ward**	**Net**
2000	0.50 (*24%*)	0.84 (*40%*)	0.79 (*36%*)	1.63 (x3.26)	**2.12**	0.25	-1.22 (x4.88)	-0.97	5.37	-25.90	-20.53
2001	0.35 (*08%*)	1.80 (*45%*)	1.83 (*47%*)	3.63 (x5.23)	**3.99**	0.18	-0.15 (x0.83)	0.02	3.77	-3.60	0.17
2002	0.45 (*26%*)	0.69 (*39%*)	0.61 (*35%*)	1.30 (x2.89)	**1.75**	0.33	-0.64 (x1.94)	-0.31	7.00	-13.74	-6.74
2003	0.59 (*17%*)	1.27 (*36%*)	1.67 (*47%*)	2.94 (x4.98)	**3.53**	0.30	-1.39 (x4.63)	-1.08	6.55	-30.53	-23.99
2004	0.29 (*11%*)	1.17 (*44%*)	1.18 (*45%*)	2.35 (x8.10)	**2.65**	0.53	-0.55 (x1.01)	-0.01	11.79	-12.16	-0.37
2005	0.37 (*16%*)	0.57 (*25%*)	1.37 (*59%*)	1.94 (x5.24)	**2.31**	0.22	-1.13 (x5.14)	-0.91	4.49	-24.52	-20.03
2006	0.74 (*24%*)	1.72 (*55%*)	0.64 (*21%*)	2.36 (x3.19)	**3.10**	0.43	-1.57 (x3.65)	-1.14	8.90	-32.43	-23.52
2007	0.59 (*43%*)	0.49 (*36%*)	0.29 (*21%*)	0.78 (x1.32)	**1.36**	0.28	-0.35 (x1.25)	-0.07	5.95	-7.27	-1.32
2008	0.45 (*16%*)	1.81 (*64%*)	0.57 (*20%*)	2.38 (x5.29)	**2.83**	0.32	-0.15 (x0.47)	0.17	6.67	-2.95	3.72
2009	0.48 (*16%*)	1.16 (*39%*)	1.30 (*45%*)	2.46 (x5.13)	**2.94**	0.46	-0.42 (x0.91)	0.04	8.96	-7.88	1.08
Mean ± *1 S.E.M.*	**0.48** (*18%*) ± *0.04*	**1.15** (*43%*) ± *0.16*	**1.03** (*39%*) ± *0.16*	**2.18** (x4.54) ± *0.26*	**2.66** ± *0.25*	0.33 ± 0.04	-0.76 (x2.30) ± 0.17	-0.43 ± 0.17	6.95 ± 0.75	16.10 ± 3.56	-9.15 ± 3.61
Average % or increase	**20%**	**42%**	**38%**	**x4.46**			x2.47				

Table S4. Seasonal and annual abundance of high-flying *migrant hoverflies*, and net northward or southward movement in each year Related to Figures 3 and 4. Numbers flying over a line of 300 km length at right angles to their direction of movement, between 150 and 1200 m above the ground

	Spring				Summer				Autumn				Total			
Year	Biomass (tons)	N (kg)	P (kg)	Energy (GJ)	Biomass (tons)	N (kg)	P (kg)	Energy (GJ)	Biomass (tons)	N (kg)	P (kg)	Energy (GJ)	Biomass (tons)	N (kg)	P (kg)	Energy (GJ)
2000	10.28	317	32	18.59	17.89	551	55	32.34	16.55	510	51	29.92	44.72	1377	138	80.85
2001	7.19	221	22	13.00	38.22	1177	118	69.10	38.19	1176	118	69.05	83.60	2575	257	151.1
2002	9.29	286	29	16.80	14.68	452	45	26.54	12.83	395	40	23.20	36.80	1133	113	66.53
2003	12.21	376	38	22.08	27.96	861	86	50.55	36.51	1125	112	66.01	76.67	2361	236	138.6
2004	6.33	195	19	11.44	26.08	803	80	47.15	25.93	799	80	46.88	58.34	1797	180	105.4
2005	7.66	236	24	13.85	12.44	383	38	22.49	29.72	915	92	53.73	49.82	1534	153	90.07
2006	15.24	469	47	27.55	35.85	1104	110	64.82	13.07	403	40	23.63	64.16	1976	198	116.0
2007	12.36	381	38	22.35	10.17	313	31	18.39	5.94	183	18	10.74	28.47	877	88	51.47
2008	9.28	286	29	16.78	36.60	1127	113	66.17	11.41	351	35	20.63	57.29	1765	176	103.6
2009	9.36	288	29	16.92	21.52	663	66	38.91	24.49	754	75	44.48	55.37	1705	171	100.1
Mean	**9.92**	**306**	**31**	**17.93**	**24.14**	**743**	**74**	**43.65**	**21.47**	**661**	**66**	**38.80**	**55.53**	**1710**	**171**	**100.4**

Table S5. Seasonal and annual wet biomass, nutrient content and energy content of high-flying *migrant hoverflies*

Related to Figures 3 and 4.

Year	**Total surviving hoverfly progeny produced by immigrants (billions)**	**Aphids consumed by surviving hoverfly progeny (trillions)**	**Estimated aphids consumed by progeny of immigrants which did not survive (trillions)**	**Total aphids consumed (trillions)**
2000	1.63	0.652	5.655	6.307
2001	3.63	1.452	3.959	5.411
2002	1.30	0.520	5.090	5.610
2003	2.94	1.176	6.673	7.849
2004	2.35	0.940	3.280	4.220
2005	1.94	0.776	4.185	4.961
2006	2.36	0.944	8.369	9.313
2007	0.78	0.312	6.673	6.985
2008	2.38	0.952	5.090	6.042
2009	2.46	0.984	5.429	6.413
Mean	**2.18**	**0.871**	**5.440**	**6.311**
± 1 S.E.M.	*± 0.26*	*± 0.103*	*± 0.476*	*± 1.212*

Table S6. Aphids consumed by the progeny of immigrant hoverflies

Related to Figures 3 and 4.

Supplemental References

S1. Aubert, J., Aubert, J-J. & Goeldlin, P. (1976). Douze ans de captures systématiques de Syrphides (Diptères) au col de Bretolet (Alpes valaisannes). Mitteilung der Schweizerische Entomologisches Gesellschaft *49*, 115–142.

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S3. Drake, V.A., Chapman, J.W., Lim, K.S., Reynolds, D.R., Riley, J.R., and Smith, A.D. (2017). Ventral-aspect radar cross sections and polarization patterns of insects at X band and their relation to size and form. Int. J. Remote Sens. *38*, 5022–5044.